Fine roots, arbuscular mycorrhizal hyphae and soil nutrients in four neotropical rain forests: patterns across large geographic distances

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Summary

• It is commonly hypothesized that stand-level fine root biomass increases as soil fertility decreases both within and among tropical forests, but few data exist to test this prediction across broad geographic scales. This study investigated the relationships among fine roots, arbuscular mycorrhizal (AM) fungi and soil nutrients in four lowland, neotropical rainforests.

• Within each forest, samples were collected from plots that differed in fertility and above-ground biomass, and fine roots, AM hyphae and total soil nutrients were measured.

• Among sites, total fine root mass varied by a factor of three, from 237 ± 19 g m^{-2} in Costa Rica to 800 ± 116 g m^{-2} in Brazil (0–40 cm depth). Both root mass and length were negatively correlated to soil nitrogen and phosphorus, but AM hyphae were not related to nutrients, root properties or above-ground biomass.

• These results suggest that understanding how soil fertility affects fine roots is an additional factor that may improve the representation of root functions in global biogeochemical models or biome-wide averages of root properties in tropical forests.

Key words: arbuscular mycorrhizal (AM) fungi, fine root mass, fine root length, soil nutrients, tropical forest.

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Introduction

Forest soils in the tropics encompass a large range of mineral nutrient availability, and above-ground primary productivity may be limited by atmospherically derived nutrients such as nitrogen (N) or rock-derived nutrients such as phosphorus (P) (Chadwick *et al.*, 1999). Similarly, below-ground biomass including fine roots (≤ 2 mm diameter), which are critical for nutrient and water uptake, may be strongly influenced by soil nutrient availability. Plants respond to limited soil nutrients by increasing biomass allocation to fine roots, by altering root morphology, or increasing fine root lifespan (Bloom *et al.*, 1985; Eissenstat & Yanai, 1997). The demonstrated plasticity in fine root properties (Reynolds & D'Antonio, 1996; Forde & Lorenzo, 2001; Hodge, 2004) leads to the prediction that stand-level fine root biomass will increase as soil fertility decreases both within (Gower, 1987) and among tropical forests (Leigh, 1999, p. 133; Maycock & Congdon, 2000), but few data exist to test this prediction across broad geographic scales. Similarly, plants are expected to maintain a larger standing crop of arbuscular mycorrhizal (AM) fungi where soil nutrients are limiting (Mosse, 1973; Read, 1991; Treseder, 2004). However, data on the abundance of arbuscular mycorrhizal (AM) fungi in tropical systems are scarce (Allen *et al.*, 1995).

Because fine roots are a dynamic component of the carbon cycle and may affect how forests respond to global changes such as increased atmospheric carbon dioxide, rising temperatures and nitrogen deposition, there is much interest in measuring

and modeling root properties at continental and global scales (Norby & Jackson, 2000). A number of reviews have examined global patterns in fine root biomass/length, dynamics, and total depth (Vogt *et al.*, 1996; Cairns *et al.*, 1997; Jackson *et al.*, 1997; Gill & Jackson, 2000; Schenk & Jackson, 2002). These reviews often group data by the biome in which they were collected, which does not account for variations within biomes that may result from differences in soil fertility, texture, rainfall seasonality and gap disturbances (Gower, 1987; Sanford, 1989; Ostertag, 1998; Silver *et al.*, 2000). Moreover, it can be difficult to draw generalizations from the literature because data come from studies that have used different definitions of fine roots and different methods for measuring fine root properties (Vogt *et al.*, 1996). Understanding the patterns of fine root distributions and their fungal symbionts within and among tropical forests and whether they vary with soil fertility is an important step to improving biome-wide fine root budgets and biogeochemical models.

This study tested the relationships among stand-level fine root distributions, AM fungi and soil nutrients at a broad geographic scale in four well studied lowland, Neotropical rain forests: La Selva (Costa Rica), Barro Colorado Island (Panama), Cocha Cashu (Peru), and Km 41 near Manaus (Brazil). Although many studies have examined variation within the forests, none have used common methods to document the patterns of soil chemical properties among the four forests (but see Vitousek & Matson, 1988). At each of the four forests we measured the stand-level distributions of fine root mass and length in three plots that differed in below-ground resource availability and above-ground biomass. Arbuscular mycorrhizal fungal hyphae, which are the dominant mycorrhizae in tropical forests (Smith & Read, 1997), were measured in three of the forests. We predicted that fine root mass (FRM), fine root length density (FRL) and lengths of AM hyphae would be greater on infertile soils, both within and among forests. We further hypothesized that the availability of rock-derived nutrients (P and cations) would be more important in determining root properties than N because many studies suggest that N does not limit net primary productivity in the forests that we studied (Denslow *et al.*, 1987; Chadwick *et al.*, 1999). Tree species composition varies among the forests (Gentry, 1990), thus, any patterns we find may include both phylogenetic and ecological causes (Nicotra *et al.*, 2002).

Materials and Methods

Study sites

Fine roots and soils were sampled from mature forests at the La Selva Biological Station (Costa Rica: 10°26′ N, 83°59′ W), Barro Colorado Island (Panama: 9°09′ N, 79°51′ W), Cocha Cashu Biological Station in Manu National Park (Peru: 11°54′ S, 71°22′ W), and the Kilometer 41 field camp of the Biological Dynamics of Forest Fragmentation Project (Brazil: 2°30′ S, 60°0′ W). Throughout the text we abbreviate these sites as LS, BCI, CC and KM41, respectively. Mean annual temperature among the forests ranges from 24 to 27°C (Powers, 2004). Mean annual precipitation (MAP) and dry season lengths (defined as the number of months with rainfall < 100 mm) show greater differences and range from: LS MAP = 4000 mm and dry season = 0; BCI MAP = 2600 mm and dry season = 4; CC MAP = 2165 mm and dry season = 3; and KM41 MAP = 2650 mm and dry season = 0 (Laurance, 2001; Leigh, 1999, p. 46; Sanford *et al.*, 1994). Even in tropical forests where average monthly precipitation exceeds 100 mm every month, there is usually some annual periodicity of rainfall. Both LS and BCI soils were sampled towards the end of the wet season (September through October 2001), CC was sampled at the end of the dry season (October 2001), and KM41 was sampled at the beginning of the wet season (November 2001).

There are large differences in soil properties among and within the forests which reflect variations in soil-forming factors (e.g. climate, parent material, topography and soil age) and the dominant soil-forming processes (e.g. *in situ* weathering, erosion, podzolization, etc.) (Chauvel *et al.*, 1987; Riley, 1994; Sollins *et al.*, 1994; Yavitt, 2000). Each site has at least two different soil orders (under US Soil Taxonomy), on which soil fertility presumably differs (Vitousek & Sanford, 1986). Detailed overviews of the sites can be found elsewhere (Powers, 2004).

Vegetation is classified as tropical wet or moist forest in all of the sites, and none of our plots have been disturbed by humans within the last 300 yr. The information on vegetation structure and composition that we have comes from concurrent studies in the same plots that we sampled (DeWalt & Chave, 2004; Harms *et al.*, 2004; J. Chave, unpublished). Density of stems = 10 cm diameter at breast height (d.b.h) and above-ground biomass (AGBM) was higher in the South American forests (CC and KM41) compared with the Central American forests (LS and BCI) (Table 1). Species richness of trees ≥ 30 cm d.b.h. in six 1400 m^2 plots within each forest was as follows: LS (23) < BCI (35) < CC (51) < KM41 (84) (J. Chave, unpublished). Of the 166 tree species identified in these plots, 30 are from the Leguminosae. These legumes are of note because they may support nitrogen-fixing bacteria that contribute total stocks of N in the forests. Abundance of individuals ≥ 30 cm d.b.h. from the legume genera reported to nodulate in Corby (1988) was highest at LS where *Pentaclethra macroloba* dominates forest composition (37 trees per 8400 m^2), intermediate at KM41 (12 trees per 8400 m^2), and low at CC (eight trees per 8400 m^2) and BCI (two trees per 8400 m^2).

Field sampling

At each of the forests, we established three 10 × 50 m plots on different soil orders that we expected to vary in fertility based upon previous work by Vitousek and Sanford (1986). They categorized Inceptisols, Alfisols, and Entisols as fertile orders and Ultisols, Oxisols and Spodosols as infertile. At LS, BCI and

Table 1 Soil order and forest structure in plots from four Neotropical forests in Costa Rica, Panama, Peru and Brazil

Forest	Plot number	Soil order	Stem density ha^{-1} (= 10 cm d.b.h)[a]	Above-ground biomass, Mg ha^{-1} (= 10 cm d.b.h)[a]	Small sapling density (individual m^{-2})[b] (10–50 cm height)
LS	1	Ultisol	420	138	0.9
	2	Ultisol	600	264	1.3
	3	Inceptisol	460	171	0.7
BCI	4	Oxisol	360	210	6.0
	5	Oxisol	420	131	6.8
	6	Alfisol	440	87	6.3
CC	7	Oxisol	700	234	15.9
	8	Oxisol	840	261	3.7
	9	Entisol	500	464	5.2
KM41	10	Spodosol	740	320	8.7
	11	Oxisol	820	248	4.5
	12	Oxisol	600	294	5.2

Sites: LS, La Selva Biological Station, Costa Rica; BCI, Barro Colorado Island, Panama; CC, Cocha Cashu Biological Station, Manu National Park, Peru; KM41, Kilometer 41 field camp of the Biological Dynamics of Forest Fragmentation Project, Brazil.
[a]DeWalt and Chave (2004).
[b]Harms *et al*. (2004).

CC, one plot was on the more fertile soil type (Alfisols, Entisols or Inceptisols) and two plots were on the less fertile soil type (Oxisols or Ultisols), which comprised a larger per cent of the total area of each field station (Table 1). At KM41, two plots were located on Oxisols and one plot was on a Spodosol. All plots were on level terrain in mature forests, avoiding treefall gaps.

Soil and root coring and processing

Each 50 × 10 m plot was subdivided into five 10 × 10 m subplots, and one sample point was placed at random within each subplot. At each sampling point, we excavated volumetric root samples from the mineral soil at four fixed depths (0–10, 10–20, 20–30 and 30–40 cm) for a total of 20 samples per plot. Several of the sample points at CC and KM41 had above-ground roots mats, which are highly efficient at retaining nutrients (Stark & Jordan, 1978). These roots were included in the samples of mineral soil from 0 to 10 cm. Although some tropical trees may have very deep roots (Nepstad *et al.*, 1994), Schenk and Jackson (2002) have estimated that 50–95% of roots in tropical evergreen forests are found in the top 15–91 cm of mineral soil. Thus, our sampling depth (0–40 cm) includes a variable but large fraction of total fine roots.

For most of the sites, soil samples were extracted with a 9.6 × 2.0 cm rectangular turf grass sampler inserted into the soil at 10 cm increments. This method worked well at all sites except BCI, where high densities of coarse roots throughout upper soil profiles prevented sampling with the turf grass sampler at many points. Therefore, for some BCI samples, we used a punch tube soil probe (inserted into the soil in 10 cm increments). For these samples, we composited seven samples extracted from a *c.* 20 × 30 cm^2 area. Estimates of fine roots made using both the methods were highly correlated (r^2 > 0.97, n = 16). Therefore regression equations were used to convert the FRM and FRL values for BCI root samples extracted with the soil probe to 'turf sampler values', and these converted values are reported to allow for direct comparison with all other data.

In the field laboratories, soil clods were broken up, each sample was well mixed in a separate plastic bag and a root-free subsample was removed from each soil sample. The root-free soil subsamples were composited by depth interval within each plot, oven-dried at approx. 60°C, and analysed for soil chemical properties as described later. From each main sample, roots were separated from soil by washing in a 0.5 mm sieve. Root length (FRL) was determined on wet roots (≤ 2 mm diameter) using the line intercept method (Newman, 1966; Tennant, 1975). Because of time constraints, no effort was made to separate live roots from dead roots, although we estimate that < 15% of any sample consisted of dead roots (J. S. Powers, personal observation). At BCI, the most seasonal forest we sampled, dead fine roots are reported to be < 8% of total FRM, even during the dry season (Yavitt & Wright, 2001). Roots were oven-dried for > 24 h at *c.* 60–70°C, and then weighed (± 0.001 g) for FRM.

Mycorrhizal hyphae

Soils from LS, BCI and CC were exported to the USA for analyses of mycorrhizal hyphae and total nutrients. Lengths of AM hyphae were determined using a modified procedure from Sylvia (1992) described in detail in Treseder and Allen (2002). Briefly, soils were dispersed in sodium metaphosphate solution (39.5 g l^{-1}), passed through a series of sieves and hyphae recovered on a 45 μm sieve. The hyphae were then collected on filters, which were examined at ×200 magnification using

a Zeiss phase-contrast microscope (Carl Zeiss, Inc., Thornwood, NY, USA). Hyphae from AM fungi were distinguished from those of non-AM fungi by examining morphology. Arbuscular mycorrhizal hyphae lack septa, tend to branch angularly and have irregular walls (Bonfante-Fasolo, 1986). Nevertheless, we note that distinctions between AM and non-AM fungi can be challenging, and this difficulty may be a source of error in our estimates. A reticule was used to measure the length of each AM hypha encountered, and total lengths of AM hyphae were expressed as mm hyphae g^{-1} soil.

Soil chemical properties

Chemical properties of soils from LS, BCI and CC were analysed using common methods. Soil pH was measured in a 1 : 2.5 soil solution ratio of deionized water using a 'Corning pH 20' meter (Corning Electrochemistry Products, Woburn, MA, USA). We compared two measurements of P and cations: total and extractable concentrations. For total nutrients, soils were digested with concentrated HNO_3 in a microwave and total P and nutrient base cations – calcium (Ca), magnesium (Mg), potassium (K) and sodium (Na) – were quantified via inductively coupled plasma electron spectroscopy at the Research Analytical Laboratory at the University of Minnesota. 'Labile' nutrients were extracted in the Mehlich III dilute acid solution and measured as above (Mehlich, 1984).

Total carbon (C) and total N were measured on finely ground soil samples following dry combustion on a Carlo Erba Elemental Analyser (Thermo Electron Corp., Milan, Italy). All nutrient concentrations are reported on an oven-dry weight basis. Because it was not possible to export soils from Brazil, samples from KM41 were analysed using standard protocols for pH in water, total C and N at EMBRAPA in Manaus (Fearnside & Filho, 2001).

Statistical analyses

We calculated pairwise Pearson correlation coefficients to explore correlations among soil chemical properties (pH, total P, sum of base cations, percentage C (%C), percentage N (%N)), fine roots (length and mass), AM hyphae length and above-ground biomass using plots as experimental units. Stepwise multiple regression was used relate FRM and FRL (from 0 to 10 cm depth) to percentage N, total P and cations, using AGBM as a covariate. Residual plots confirmed that the response variables did not require data transformations. All analyses were performed with S-PLUS 2000 (Mathsoft, Inc., Seattle, WA, USA).

Results

Patterns of soil nutrients

As expected, Mehlich-III extractable P and cations were a smaller fraction of total nutrients (Fig. 1). However, extractable P was not well correlated with total P (Fig. 1a), although cations were positively related to one another (Fig. 1b). The poor correlation between extractable and total P may be an artifact of soil drying. Therefore, we made the assumption that total nutrient pools provide a better time-integrated index of relative nutrient availability among sites than extractable pools, and do not discuss extractable nutrients further.

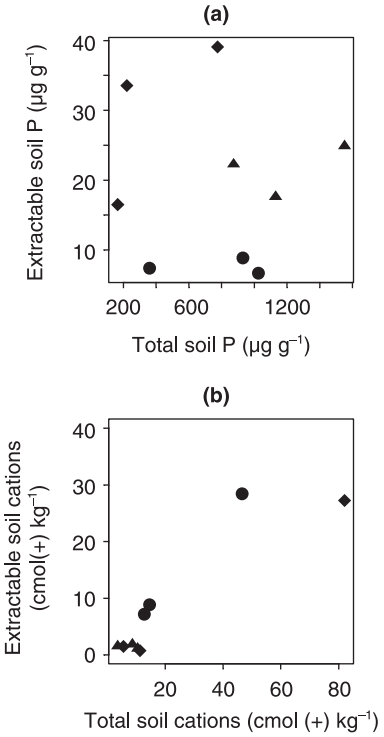

Fig. 1 Relationships between total and Mehlich-III extractable soil P (a) and soil cations (b). Triangles, LS (La Selva Biological Station, Costa Rica); circles, BCI (Barro Colorado Island, Panama); diamonds, CC (Cocha Cashu Biological Station, Manu National Park, Peru).

There were large differences in total nutrients, pH and %C among sites (Table 2). In particular, base cation concentrations were extremely variable, ranging from 2- to 76-fold differences among plots for the 0–10 cm sampling depth. Not surprisingly, among sites both cations and pH were significantly correlated, as were total C and N (Table 3). Total P was positively correlated with total C and N, with Pearson correlation coefficients of 0.77 ($P < 0.012$) and 0.78 ($P < 0.012$), respectively (Table 3). The soils from La Selva are comparatively high in P, but low in total base cations. By contrast, soils from BCI appear to be high in Ca but low in P, a pattern also found in the nearby Gigante Peninsula (Cavelier, 1992). Soils at CC showed a different pattern. The alluvial Entisol formed from recently deposited sediment from the Andes had intermediate P, very high base cation concentrations and near-neutral pH, in contrast to the extremely weathered, terra firme Oxisols. It is interesting to note that the soils from Brazil had higher %C and %N than the Peruvian Oxisols (Table 2). See the supplementary material Tables S1–S4 for soil chemical data from other soil depths.

Table 2 Soil chemical properties in plots on different soil orders in four neotropical forests

Forest	Plot number	pH_{water}	C (%)	N (%)	P (μg g^{-1})	Ca (cmol (+) kg^{-1})	K (cmol (+) kg^{-1})	Mg (cmol (+) kg^{-1})	Na (cmol (+) kg^{-1})
LS	1	4.0	5.77	0.49	873	0.96	1.30	7.76	0.43
	2	4.1	4.70	0.42	1129	1.19	0.31	2.04	0.11
	3	3.9	4.77	0.45	1552	1.66	1.31	5.34	0.28
BCI	4	5.6	4.25	0.42	931	10.29	0.59	3.50	0.22
	5	5.3	3.93	0.40	1025	6.25	0.58	5.86	0.15
	6	5.5	3.65	0.36	361	23.59	0.59	22.16	0.30
CC	7	4.5	0.83	0.09	221	1.39	1.90	2.12	0.06
	8	3.8	0.30	0.03	167	0.53	5.31	5.09	0.40
	9	6.7	4.45	0.43	777	40.35	8.36	32.97	0.35
KM41	10	4.3	1.94	0.11					
	11	4.1	3.92	0.26					
	12	4.4	3.68	0.24					

Sites: LS, La Selva Biological Station, Costa Rica; BCI, Barro Colorado Island, Panama; CC, Cocha Cashu Biological Station, Manu National Park, Peru; KM41, Kilometer 41 field camp of the Biological Dynamics of Forest Fragmentation Project, Brazil.
All data are for the 0–10 cm depth intervals. Nutrient data are total concentrations.

Table 3 Pearson's correlation coefficients between soil chemical variables, fine root mass (FRM), fine root length (FRL), arbuscular mycorrhizal (AM) hyphae and above-ground biomass (AGBM) in four neotropical forests

	Cations	pH	%C	%N	FRM	FRL	AM hyphae	AGBM
Total P	−0.17 (0.65)	−0.08 (0.83)	**0.77 (0.014)**	**0.78 (0.012)**	**–0.77 (0.015)**	**–0.77 (0.014)**	−0.25 (0.52)	−0.08 (0.85)
Cations		**0.83 (0.006)**	0.17 (0.66)	0.22 (0.58)	0.21 (0.59)	−0.08 (0.85)	0.30 (0.43)	0.54 (0.13)
pH			0.20 (0.54)	0.35 (0.27)	−0.23 (0.48)	−0.18 (0.58)	0.11 (0.78)	0.29 (0.36)
%C				**0.95 (< 0.0001)**	−0.35 (0.27)	**–0.79 (0.003)**	0.17 (0.66)	−0.18 (0.57)
%N					−0.57 (0.054)	**–0.85 (0.0004)**	0.12 (0.75)	−0.26 (0.42)
FRM						**0.71 (0.010)**	−0.03 (0.93)	0.38 (0.23)
FRL							−0.22 (0.57)	0.35 (0.26)
AM hyphae								0.20 (0.60)

P-values are in parentheses. Soil and root properties were measured in 0–10 cm soil depth. Degrees of freedom are 7 for comparisons involving hyphae, cations and/or P, and 10 otherwise. Correlations with *P*-values < 0.05 are in bold type.

Fine roots and AM hyphae in relation to soil nutrients

Average fine root mass and fine root length density declined consistently with depth in the soil profile at all sites (Fig. 2), but did not reach zero. This suggests that fine roots exist in all forests below 40 cm depth, but also that our surface sampling of roots stocks is a relatively constant proportion of total roots in each plot, allowing for comparisons among sites. There was over a threefold variation in cumulative FRM (g m^{-2}) in the top 40 cm of soil among sites (± 1 SE, n = 3): LS = 237 ± 19, BCI = 278 ± 20, CC = 497 ± 45 and KM41 = 800 ± 116. As expected, FRM and FRL were positively correlated to one another, but these estimates of surface root biomass (0–10 cm) were not correlated with above-ground biomass (Table 3). Both FRM and FRL were strongly, negatively related to total soil P and %N (Table 3, Fig. 3). However, the strength of these correlations differed for root mass and length. The FRM was better correlated to soil P than %N (Pearson's correlation coefficient of –0.77 vs –0.57, respectively). By contrast, FRL was better correlated to soil N (Pearson's correlation coefficient = −0.85) than soil P (–0.77). Multiple regression analyses did not include the sites from Brazil because of the lack of data for cations and P. In this restricted data set, %N was the only variable that explained variation in FRM ($F_{1,7}$ = 25.19, r^2 = 0.78, P = 0.002) and FRL ($F_{1,7}$ = 35.37, r^2 = 0.83, P = 0.0006); cations, P and AGBM were not retained in the regression models.

Mean AM fungal hyphae lengths (0–10 cm) were highly variable within each forest: LS = 156 ± 62, BCI = 149 ± 73, and CC = 153 ± 67 (mm g^{-1} soil ± 1 SE, n = 3 plots per forest). The AM hyphal lengths were generally higher in the upper soil layers (see the supplementary material Tables S1, S2 and S3), and were lowest at BCI in soil depths from 10 to 40 cm. There were no significant correlations between AM hyphae lengths and soil chemical properties, root traits or AGBM (Table 3).

Discussion

From Central America to Central Amazonia, we found a threefold range of variation in fine root stocks in our single sampling period and a strong negative correlation between

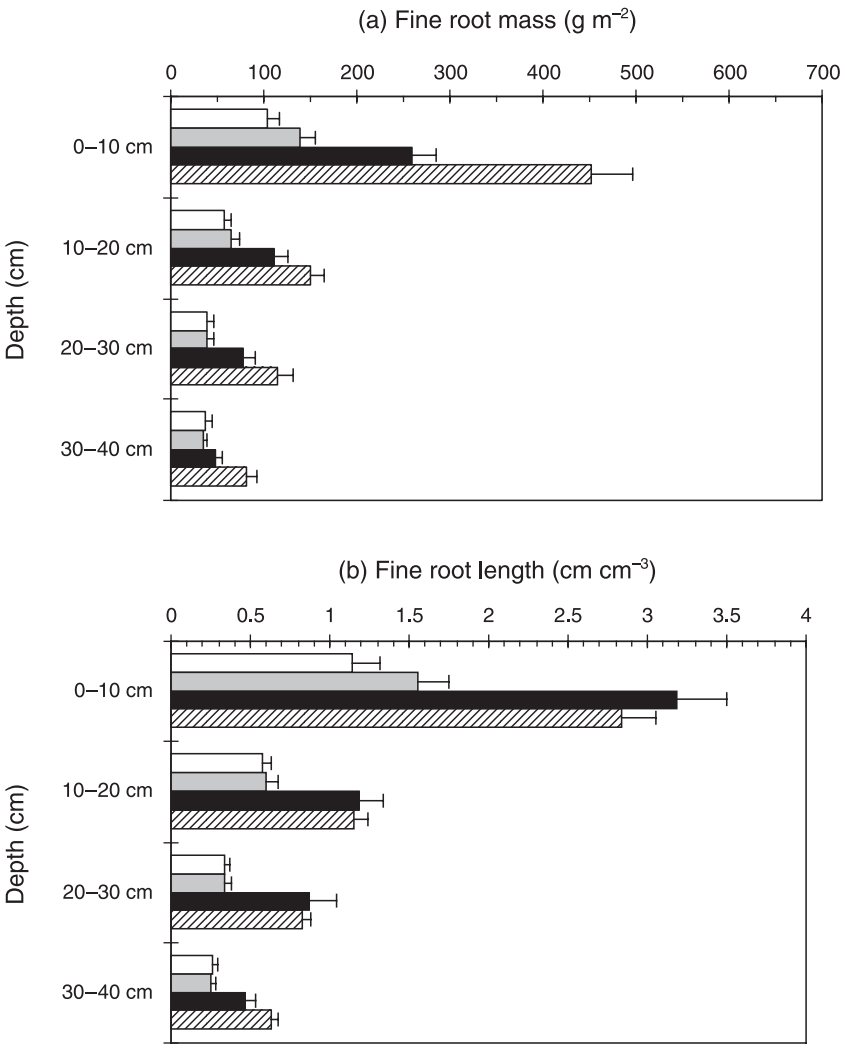

Fig. 2 (a) Average fine root mass, and (b) fine root length density by depth in four Neotropical forests (error bars are 1 SE of the mean), n = 15 per site and depth. Open columns, La Selva Biological Station, Costa Rica; tinted columns, Barro Colorado Island, Panama; closed columns, Cocha Cashu Biological Station, Manu National Park, Peru; hatched columns, Kilometer 41 field camp of the Biological Dynamics of Forest Fragmentation Project, Brazil.

fine roots and soil nitrogen and phosphorous concentrations. We found little evidence, however, for either fine roots or soil nutrients to be correlated with AGBM or AM fungal hyphae. The large interforest variation and relationship between roots and soil nutrients have important implications for understanding the controls over fine roots, for estimating below-ground carbon distribution in tropical soils and for predicting the consequences of environmental changes on root stocks and dynamics.

Jackson *et al.* (1997) compiled a global database of fine root biomass for different biomes, including 12 observations for tropical evergreen forests. Our values of FRM bracket Jackson's tropical evergreen forest average of 570 ± 69 (SEM) g m^{-2} FRM in the top 30 cm soil, but show considerably more variability. Some of this variability is negatively correlated with variation in soil nutrient concentrations (Fig. 3). These results are consistent with other tropical and temperate studies of FRM along natural fertility gradients (Gower, 1987; Ostertag, 1998; Maycock & Congdon, 2000) and under fertilization (Gower & Vitousek, 1989).

The four forests differ clearly with respect to soil nutrients, however, there are other important differences in climate and species composition among sites that may also affect root properties. Although our data do not allow us to partition the variation in root stocks among forests into these components, it is interesting to note that LS and BCI vary greatly in mean annual precipitation and dry season length, but have relatively fewer differences in soil nutrients (Fig. 3). They also stand out as the forests with the lowest root stocks. By contrast, LS and KM41 are both relatively aseasonal (both have no months with rainfall < 10 cm), but have large differences in total nutrients and a threefold difference in fine root stocks. Taken together these pairwise comparisons suggest a large influence of soil nutrients on root stocks in these forests.

We found several unexpected results when examining the correlations between root traits and individual nutrients. First, total soil N and P were positively correlated with one another, but not with total nutrient cations. Although both N and P change over the course of soil development, they are not

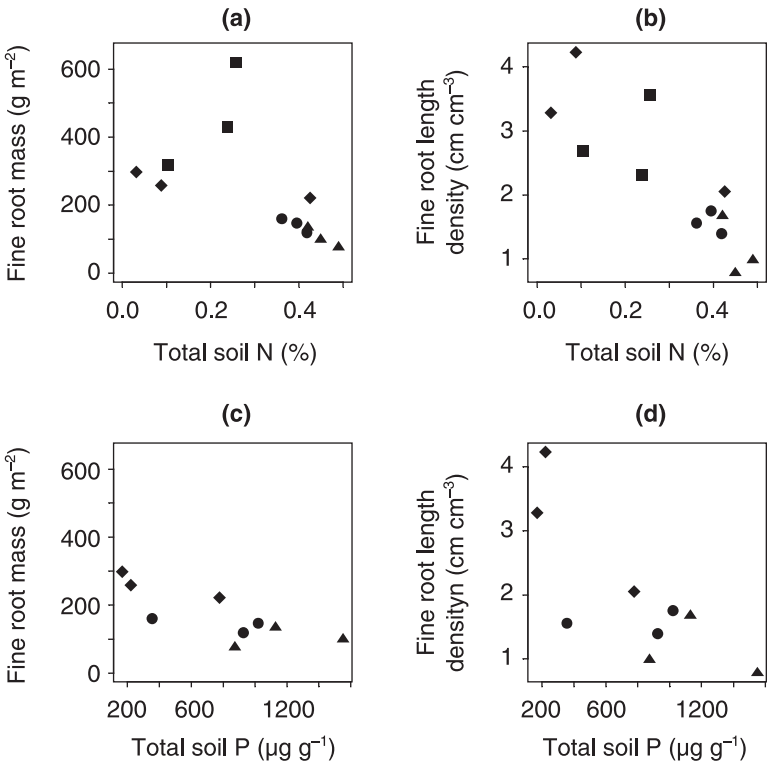

Fig. 3 Fine root mass and fine root length density (0–10 cm) in relation to total soil nitrogen (N) (a,b) and total phosphorus (P) (c,d). Triangles, LS (La Selva Biological Station, Costa Rica); circles, Barro Colorado Island, Panama; diamonds, Cocha Cashu Biological Station, Manu National Park, Peru; squares, Kilometer 41 field camp of the Biological Dynamics of Forest Fragmentation Project, Brazil.

expected to covary, as they have different ultimate sources and biogeochemical controls (Walker & Syers, 1976). Second, soil N was as good a predictor of root traits as P. While total soil N may not be the best measure of N availability, there is direct evidence that N availability declines from La Selva soils to those near Manaus, Brazil (Vitousek & Matson, 1988). Because many tropical forests are located on highly weathered landforms, it is often assumed that rock-derived nutrients such as P and Ca are more important controls on above-ground primary productivity than N. Our results provide strong support that N is a key control on fine root distributions in tropical rain forests across large spatial scales and underscore that there remains much to be learned about the relationships between soil nutrients and ecosystem processes in tropical forests.

The negative relationship between soil nutrients and roots does not appear to reflect differences in investment to AM fungi; we found no evidence that AM hyphal lengths were correlated with either soil nutrients or root abundance. In addition, standing stocks were generally low compared with those of other tropical forests (Treseder & Allen, 2002), grasslands (Tisdall & Oades, 1979; McNaughton & Oesterheld, 1990), and greenhouse experiments (reviewed in Smith & Read, 1997), which typically contain one or more meters of hyphae per gram soil. In our study sites, plants may rely primarily on roots for nutrient uptake and might not cultivate AM fungi in response to nutrient limitation. Fungal symbionts in these systems may confer alternative benefits such as tolerance to high levels of aluminum (Lux & Cumming, 2001). The reduction in AM hyphal length at depths below 10 cm is consistent with patterns observed in other field studies (Cooke *et al.*, 1993; Brown & Bledsoe, 1996; Ingleby *et al.*, 1997). In our sites, the decline may be related to the reduction in root biomass with depth.

Many studies in other tropical forests have reported that both fine root stocks and production are higher during the wet season (Yavitt & Wright, 2001; Kummerow *et al.*, 1990; Roy & Singh, 1995). A major limitation of our study is that we sampled only a single period because of logistical constraints. It is possible that our results are influenced by differences in the season in which we collected our data. However, seasonal differences in root production and decomposition at these sites would tend to minimize the differences in root stocks among these forests, i.e. the forests with lowest root stocks, LS and BCI, were sampled during the wet season when root stocks should be highest, while the forests with highest roots stocks, CC and KM41 were sampled at the end of the dry season and the beginning of the wet season, respectively, when root stocks should be lower.

In conclusion, our broad geographic sampling of fine roots, soil nutrients and AM hyphae in evergreen tropical forests revealed strong correlations between fine roots and soil N and P, but no patterns for AM hyphae. These intriguing results lead to further hypotheses about which nutrients are important for root processes in lowland tropical forests, the degree to which root stocks are uncoupled from above-ground biomass, the

possibility that above- and below-ground plant process may be limited by different nutrients, and controls on the abundance of fungal symbionts in these forests. Together, these results suggest that understanding how soil fertility affects fine roots is an additional factor that may help to improve the representation of root functions in global biogeochemical models or biome-wide averages of root properties in tropical forests.

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Supplementary material

The following material is available as supplementary material at http://www.blackwellpublishing.com/products/journals/suppmat/NPH/NPH1279/NPH1279sm.htm

Table S1 Total soil nutrients, fine root mass (FRM), fine root length (FRL) and arbuscular mycorrhizal (AM) fungal hyphae by depth from three plots at La Selva, Costa Rica.

Table S2 Total soil nutrients, fine root mass (FRM), fine root length (FRL) and arbuscular mycorrhizal (AM) fungal hyphae by depth from three plots at Barro Colorado Island, Panama.

Table S3 Total soil nutrients, fine root mass (FRM), fine root length (FRL) and arbuscular mycorrhizal (AM) fungal hyphae by depth from three plots at Cocha Cashu, Peru.

Table S4 Total soil nutrients, fine root mass (FRM) and fine root length (FRL) by depth from three plots at KM41, Brazil.

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